广东苏铁及中国东南部几种苏铁的研究:

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ON CYCAS TAIWANIANA CARRUTHERS (CYCADACEAE) AND THE CYCADS OF SOUTH-EASTERN CHINA

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Abstract A descriptive account of morphology and anatomy of the naturally-occurring cycads of south-eastern China (Hainan, Guangdong and Taiwan) is presented, with a key, illustrations, and discussion of their relationships.

Key words Cycas taiwaniana; C. taitungensis; C. hainanensis; Subsect. Taiwanianosae; Anatomy

抽要 本文对华东南(台湾,广东,海南)产的广东苏铁、台东苏铁及海南苏铁的形态学、解剖学和分 类学问题、以及这几种苏铁的亲缘关系进行了讨论。本文附有检索表及图。

关键词 广东苏铁;台东苏铁;海南苏铁;广东苏铁亚组;解剖学

Introduction

Together with colleagues, we have recently shown that plants of the genus Cycas occurring on Taiwan are specifically distinct from those occurring on Mainland China (Shen et al., 1994). The name C. taiwaniana long misapplied to the Taiwanese plant is in fact based on a plant from mainland China, and the Taiwanese plant was undescribed until 1994. Although nearest neighbors geographically, the two different species are in fact widely separated in relationships, and belong to two distinct sections within the genus. We have discussed misapplication of the name Cycas taiwaniana elsewhere, and provided a new name for the

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Taiwan cycad (Shen et al., op cit.). The nomenclatural confusion was realised independently by three separate workers. Chen in Mainland China first observed that the Mainland and Taiwanese plants were specifically distinct, then Hill in Australia noted that the type of C. taiwaniana did not belong to the Taiwan plants. Shen and Tsou working in Taipei made the same observations and expressed agreement with the previous workers (in letters). Observations from the four workers have been combined in the publication of the name Cycas taitungensis Shen, Hill, Chen & Tsou (Shen et al., 1994). Further observations on anatomy and infrageneric relationships are presented herein, together with a key to the species of southeastern China and descriptions of the three species occurring in that region.

Morphology and Anatomy

The Chinese cycads are all characterised by a broad, deeply pectinate megasporophyll lamina (Plate 1, figs. 4, 6), and a broadly rounded 'cabbage-like' female cone. However, seed and ovule morphology varies greatly, with two distinct forms occurring. The native Taiwanese cycad has densely tomentose ovules, and elongate, orange-red seeds with a smooth or longitudinally grooved sclerotesta. In contrast, the mainland and Hainanese cycads have wholly glabrous ovules, and sub-globular, yellow seeds with a verrucose sclerotesta.

Leaf anatomy also differs, the Taiwanese cycad having thick pinnae (0.5 mm thick) with both upper and lower mesophyll continuous across the midrib, uninterrupted upper hypodermis, deeply sunken stomata with over-arching subsidiary cells, and a thickened cuticle (figs. 1, 2). The midrib in *C. taitungensis* is not or scarcely raised above the lamina on the upper (adaxial) surface, and very prominently raised below.

The conditions of uninterrupted upper hypodermis, continuous mesophyll, midrib raised below, thickened cuticle, and deeply sunken stomata also occur in the closely related C. revoluta from Japan, and are parallelled in C. beddomei from India (Rao, 1974) and several species from Australia (e. g. C. cairnsiana, C. calcicola, C. pruinosa, Hill, in prep.). These taxa, however, all possess narrow, strongly recurved to revolute pinna margins, whereas C. taitungensis has more or less flat pinnae. The Japanese-Chinese, Indian and Australian groups of taxa differ markedly from each other in many other respects, and are placed in different sections within the genus (Hill, 1994). The distinctive characteristics of leaf anatomy are thought to be advanced characters, and consequently similarities in leaf anatomy must be regarded as parallel developments. The suite of characters developed is consistent with ecological adaptation to the drier and harsher environments in which all of these taxa (including C. taitungensis) occur.

C. taitungensis possesses seemingly more primitive broader, flat pinnae, but otherwise shares the characters seen in C. revoluta, as discussed above. It would appear from this that C. taitungensis has evolved from stock of the C. revoluta type, and that the apparently primitive flat pinnae are in fact a reversal from the revolute ancestral condition.

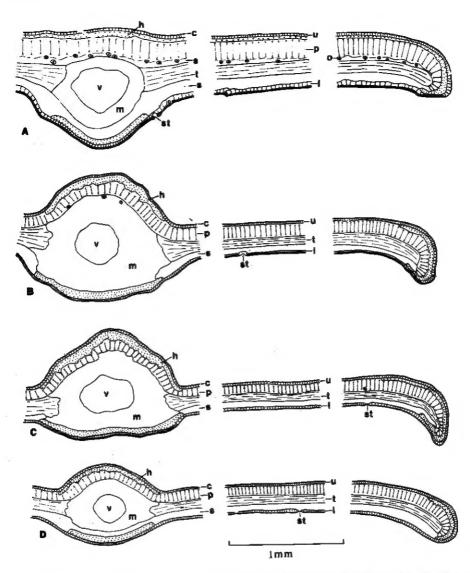


Fig. 1 Transverse sections of adult pinnae. A. C. taitungensis (from Walkley NSW 265951); B. C. taiwaniana (from the type, Hance herbarium in BM, no. 14119); C. C. taiwaniana (from PE 1105720); D. C. hainanensis (from the type, Zhong 4706).

c. cuticle; h. hypodermis; m. midrib sheathing tissue; l. lower epidermis; o. oxalate crystals; p. palisade mesophyll; s. compact mesophyll; t. undifferentiated transfusion tissue; u. upper epidermis; m. sclerenchymatous midrib vascular bundle sheathing tissue; st. stomatal opening; v. midrib vascular bundle. Scale bar=1 mm.

The mainland and Hainanese cycads have thin pinnae (less than 0.35 mm thick) with reduced or no hypodermis across the lamina (i. e. the section of the pinna lying between but not including the midrib and the thickened margin), open, shallow stomatal crypts, and thin cuticle. The mainland taxon shows continuous mesophyll only on the upper surface, whereas the Hainanese species has continuous upper and lower mesophyll. The midrib in both taxa is prominently raised on the upper (adaxial) surface, and raised but less prominently so on the lower surface.

The south-eastern Chinese cycads thus segregate into two quite distinct groups that have been recognised as distinct sections within the genus (Schuster, 1932; Hill, 1994). Distinguishing characters of the sections are presented, and the species are placed in their respective groups and individually described below.

Key to the sections and species of south-eastern China

- Ovules tomentose; apical megasporophyll spine not clearly distinct from lateral spines; sclerotesta not verrucose
 A. Section Asiorientales 1. C. taitungensis
- Ovules glabrous; apical megasporophyll spine clearly larger and broader than lateral spines; sclerotesta verrucose
 B. Section Indosinenses
 - 2. Pinnae less than 12 mm wide; abaxial mesophyll continuous across midrib; seeds 35—40 cm long
 2. C. hainanensis
 - Pinnae more than 13 mm wide; abaxial mesophyll not continuous across midrib; seeds 28—33 cm long
 3. C. taiwaniana

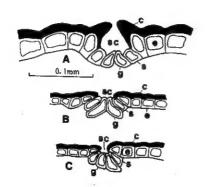


Fig. 2 Sections of stomata. A. C. taitungensis (from Walkley NSW 265951); B. C. taitungensis (from the type, Hance herbarium in BM, no. 14119); C. C. hainanensis (from the type, Zhong 4706). c. cuticle; e. epidermal cell; g. guard cell; s. subsidiary cell; sc. stomatal crypt.

Scale bar = 0.1 mm.

A. Section Asiorientales Schuster in Engler, Pflanzenr. 99, 4 (1): 65, 81, 1932.

Type: C. revoluta Thunberg; the single species in the section as defined by Schuster.

This section is uniquely defined by the tomentose ovules. The broad, deeply pectinate megasporophyll lamina groups the section with other sections occurring primarily in Mainland Asia, although this may well be a shared primitive character. The arborescent habit is also probably a shared primitive character. The section is composed of only two closely related species, Cycas revoluta and the following. Natural distribution of this section is limited to southern Japan and Taiwan, with uncorroborated reports of C. revoluta from Fukien Province in Mainland China (Chen et al., 1994).

1. Cycas taitungensis C. F. Shen, K. D. Hill,

C. H. Tsou & C. J. Chen in Bot. Bull. Acad. Sin. 35: 133—140, fig. 1. 1994. — C. taiwaniana auct. non Carruth.: Yamamoto, Suppl. Icon. Pl. Form. 4: 3. 1928; Li, Fl. Taiwan 1: 496, pl. 170a, b. 1975; S. H. Fu et al. in Cheng et L. K. Fu, Fl. Reip. Popul. Sin. 7: 9. 1978, p. p., quoad pl. Taiwan. — C. revoluta Thunb. var. taiwaniana (Carruth.) Schuster in Engler, Pflanzenr. 99, 4 (1): 84. 1932, p. p., quoad pl. Taiwan.

Stem to 2 m tall, rarely to 5 m, 20—45 cm diam. Leaves 80—180 cm long, openly keeled in section (opposing pinnae inserted at 110—150° on rachis), rachis usually terminated by a spine, with 200—400 pinnae; petiole sparsely pubescent when young, gradually becoming glabrous, spinescent throughout, 10—25 cm long; median pinnae at 45—65° to

rachis, 120-180 mm long, 5.0-7.5 mm wide, 0.5-0.6 mm thick, glossy slightly bluish deep green, more or less keeled in section with flat or slightly recurved margins, decurrent for 2.5-5.0 mm, narrowed to 2.0-3.0 mm at base (25-35% of maximum width), spaced at 5-8 mm on rachis, apex attenuate, pungent; midrib not or slightly raised above, prominent below. New growth densely tomentose with orange-brown trichomes. Cataphylls densely pale brown-tomentose, 6-12 cm long, hard and pungent, with thick loose pale brown wool between. Microsporangiate cones elongate-ovoid, 35-60 cm long, 8.5-12 cm diam. Microporophyll lamina 35-40 mm long, 11-13 mm wide; sterile apex 6-8 mm long, not recurved, apical spine absent or highly reduced, less than 4 mm long, not upturned. Megasporophylls 18-28 cm long, bright orange-red, pale brown-tomentose, with 3-6 ovules; sterile apex 90-140 mm long, 70-110 mm wide, broadly ovate, regularly pectinate, with 26-38 lateral spines, apical spine 20-35 mm long, 2-3 mm wide, lateral spines 35-45 mm long, 2-3 mm wide; ovules (1-) 2 (-3) on each side, densely pale brown-tomentose. Seeds elongate-ovoid or ellipsoid, slightly flattened, green maturing to orange-red, becoming purplish-red and rugose when dry, densely or loosely pale brown-tomentose, not pruinose, 38-46 mm long, 28-34 mm diam.; sarcotesta 2-3 mm thick. Fig. 3.

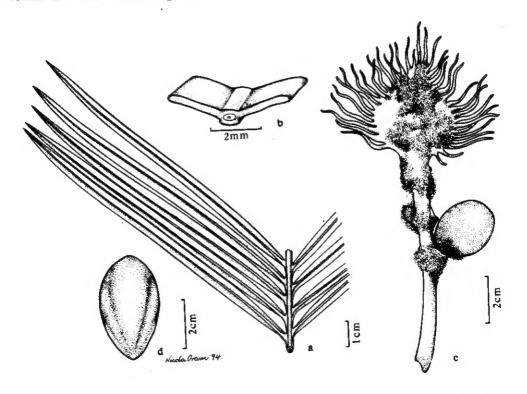


Fig. 3 Cycas taitungensis. a. part of frond; b. section of pinna; c. megasporophyll; d. seed (a, b from Hsieh 2 Mar 1993 (PE 1570322), c from Tsou Sept 1992 (PE 1581385), d from Walkley NSW 265951). Scale bar: a=1 cm; b=2 mm; c, d=2 cm

Distribution: endemic in south-eastern Taiwan, Taidung district, in the Coastal Range and the Lu-yeh Valley (fig. 4). Substantial wild populations of this species are conserved in the Taidung Hong-ye Village Taiwan Cycas Nature Reserve (Osborne, 1989).

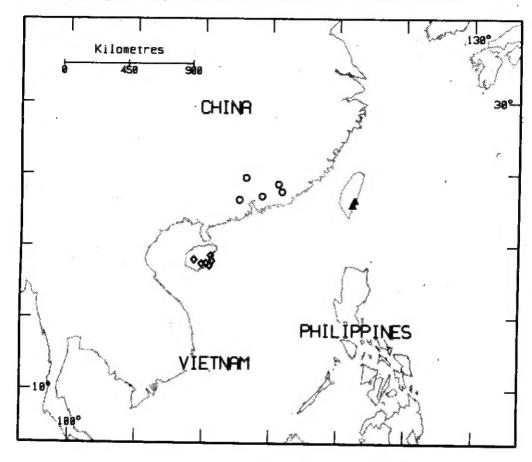


Fig. 4 Distribution of Cycas taitungensis (triangle), C. taiwaniana (circle), C. hainanensis (diamond).

Notes: Nearest to Cycas revoluta, with which it shares the tomentose ovules, this species is readily distinguished from C. revoluta by the much more open habit with longer, broader and flatter (less keeled) leaves with longer, broader, flatter and non-revolute pinnae (leaves are 50—100 cm long and keeled at 60—20°, with pinnae revolute, 60—80 mm long and 3—6 mm wide in C. revoluta), and the more or less smaller and purplish-red seeds with elongate, longitudinally irregularly grooved sclerotesta. It has been included in the synonymy of Cycas revoluta by some authors (under the misapplied name C. taiwaniana e. g. Schuster, 1932). Seed was made available from the Taidung Hong-Ye Village Taiwan Cycas Nature Reserve in south-eastern Taiwan during the 1980's, and this species is now common in cultivation throughout the world.

Selected specimens: Taiwan: Taidung County, inter Sesui et Matuyama, Yamamoto &

Goto, 28 Dec 1928 (TAI 194156, TAI 194157, TAI 194159); Taidung, Hsieh & Tsou s. n. Nov 1992 (PE); Tsou s. n. Sept. 1992 (PE). Cult.: Burpengary, Queensland, Australia, from seed from Taidung, Taiwan, Walkley NSW 265951, Feb 1993 (NSW); Ningyang, Fujian, China, from Taidung, Taiwan, Lin 5562 (PE); Xianhe Bot. Gard., Shenzen, China, from Taidung, Taiwan, Chen 92589 (PE); Garden of Taiwan University, Hsieh s. n. 2 Mar 1993 (PE).

B. Section Indosinenses Schuster in Engler, Pflanzenr. 99, 4 (1): 65, 80. 1932. Type: C. siamensis Miquel, lectotype designated by Hill (1994).

Distinguishing characteristics of this section are the pectinate megasporophyll lamina with a broadened apical spine or extension, the glabrous ovules, and the arborescent habit. This section shows striking internal differences in seed morphology, with at least four distinct groups known. These may be recognised as subsections, one of which occurs in southeastern China.

The section is widely distributed, extending from north-east India and Nepal east through southern China to Guangdong and Hainan Provinces, and south to Peninsular Malaysia and Palawan in The Philippines. The total number of species involved is unclear, with possibly up to 12 or more species.

Subsection Taiwanianosae K. D. Hill & C. J. Chen, subsect. nov.

Ab Subsect. Indosinensibus habitu arborescente et sclerotesta verrucosa distinguitur.

Type: Cycas taiwaniana Carruthers.

This group is defined by the combination of the verrucose sclerotesta and the arborescent habit. Two taxa are included, as presently understood, with considerable variation that requires further study. The group is endemic in south-eastern China, with one species in Hainan and one in Guangdong.

C. micholitzii Dyer from northern Vietnam and Guangxi and Yunnan Provinces and the plants from Thailand and Yunnan Province that have been identified as C. micholitzii Dyer var. simplicipinna Smitinand share the verrucose seeds. However, several of the characters shown by the C. micholitzii and the C. taiwaniana groups are apparently shared primitive characters, and do not clearly elucidate relationships. The C. micholitzii group is uniquely difined by the subterranean habit, the reduced megasporophyll and the small, narrow male cone, and has been regarded as a separate section on this basis (Smitinand, 1971). The verrucose sclerotesta is regarded as a primitive character, and subsection Taiwanianosae is grouped in section Indosinenses by the broadened apical spine or extension of the megasporophyll lamina.

2. Cycas hainanensis C. J. Chen ex W. C. Cheng, L. K. Fu & C. Y. Cheng in Acta Phytotax. sin. 13 (4): 82, fig. 2 (5-6). 1975.

Type: Hainan; Luilianling, Wangning County, Y. Zhong 4706, 16 Oct 1961 (holotype, PE; isotype, IBSC).

Stem to 1.5 m tall, rarely to 2.5 m, 15—25 (—35) cm diam. Leaves 65—200 cm long, keeled in section (opposing pinnae inserted at 90—130° on rachis), with 130—170 pinnae; petiole glabrous, spinescent throughout, 20—35 cm long; median pinnae at 60—80° to rachis, 130—320 mm long, 5.5—12.0 mm wide, 0.25—0.3 mm thick, glabrous, glossy green, flat in section with slightly recurved margins, decurrent for 2.0—4.0 mm, narrowed to 2.0—4.0 mm at base (25—40% of maximum width), spaced at 8—15 mm on rachis, apex acute; midrib prominently raised above, not or slightly raised below. New growth densely tomentose with orange trichomes. Cataphylls not known. Microsporangiate cones not known. Megasporophylls 16—20 cm long, orange-brown-tomentose, with 1—4 ovules, sterile apex 70—100 mm long, 40—70 mm wide, ovate, regularly deeply dentate, with 10—24 lateral spines, apical spine oblong-flattened, 20—35 mm long, 7—20 mm wide, lateral spines 20—35 mm long. Seeds subglobular, green maturing to yellow, not pruinose, 35—40 mm long, 30—36 mm diam.; sarcotesta 1.5—2.5 mm thick; sclerotesta regularly finely verrucose. Fig. 5.

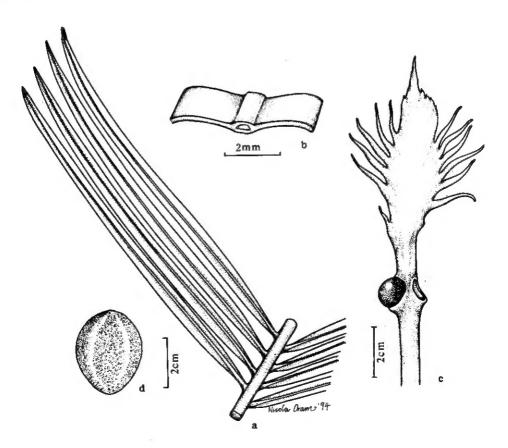


Fig. 5 Cycas hainanensis. a. part of frond; b. section of pinna; c. megasporophyll; d. seed (a, b, c from Zhong 4706, d from NSW 271211). Scale bar; a, c, d=2 cm; b=2 mm.

Distribution: China (Hainan, fig. 4). Known only from Hainan Island. Wild populations are now very restricted, and this species survives mainly in cultivation.

Notes: C. hainanensis is very close to C. taiwaniana (below), differing in the more keeled leaves with narrower and more crowded pinnae, and the smaller megasporophyll lamina with fewer but longer lateral spines and a greatly expanded apical spine. Considerable variation is evident in specimens from Hainan, and further study is required in this region. This species is native to closed mesophyll forests (Zhou et al., 1990), and some of the variation evident may be from more exposed growth conditions under cultivation.

Selected specimens: Hainan: Luilianling, Wangning County, Tang 92586 (PE); southern Wanning County, Yang NSW 271211, 30 Oct 1992 (NSW); Qiongdong County, Liang 68119 (IBSC); Baoting County, Liang 68300 (IBSC); Mt Diaolou, Lingshui County, Hainan Expedition, 1959 (PE); Bawangling, Changjiang County, C. J. Chen 92606 (PE). Cult: Haikou Peoples Park, Haikou, Hainan, S. H. Chun 17629 (IBSC, PE).

3. Cycas taiwaniana Carruthers in J. Bot. 31: 2, t. 331. 1893. — Cycas revoluta Thunberg var. taiwaniana (Carruthers) Schuster in Engler, Pflanzenr. 99, 4(1): 84. 1932.

Type: "Ex insula Formosa, autumn 1867", R. Swinhoe (holotype, BM, numbered 14112, photo NSW, PE (Plate 1), isotype, K). This collection did not come from Taiwan [= "Formosa"], and was probably from eastern Guangdong Province (near Shantou). Typification and the original collection site is discussed by Thiselton-Dyer (1902) and Shen et al. (1994).

Stem to 4 m tall, rarely to 7 m, 12—25 (—30) cm diam. Leaves 180—300 cm long, flat in section (opposing pinnae inserted at 150—180° on rachis), with 100—180 pinnae; petiole glabrous, spinescent throughout, 30—120 cm long; median pinnae at 45—55° to rachis, often falcate, 180—350 mm long, 13.0—18.0 mm wide, 0.25—0.35 mm thick, glabrous, glossy green, flat in section with very slightly recurved margins, decurrent for 2.5—6.0 mm, narrowed to 2.5—4.0 mm at base (20—33% of maximum width), spaced at 7—14 mm on rachis, apex attenuate; midrib prominent above and below when fresh, slightly raised below when dry. New growth densely tomentose with orange trichomes. Cataphylls not known. Microsporangiate cones ovid-cylindric 30—45 cm long, 8—10 cm diam. Microsporophyll lamila 3—4 cm long; sterile apex 7—10 mm long, apical spine short. Megasporophylls 16—20 cm long, grey- and orange-tomentose, with 2—4 ovules, sterile apex 70—120 mm long, 55—70 mm wide, ovate, regularly deeply dentate, with 26—30 lateral spines, apical spine acute, 20—35 mm long, 5—8 mm wide, lateral spines 12—18 mm long. Seeds subglobular, maturing to yellow, not pruinose, 28—33 mm long, 25—30 mm diam.; sarcotesta 2.5—4 mm thick; sclerotesta regularly finely verrucose. Fig. 6.

Distribution: apparently endemic in Guangdong Province, China (fig. 4). This species has long been cultivated in Guangdong and Fujian Provinces, and may also have been originally native in the latter. It is now common in cultivation, and most collections, if not all,

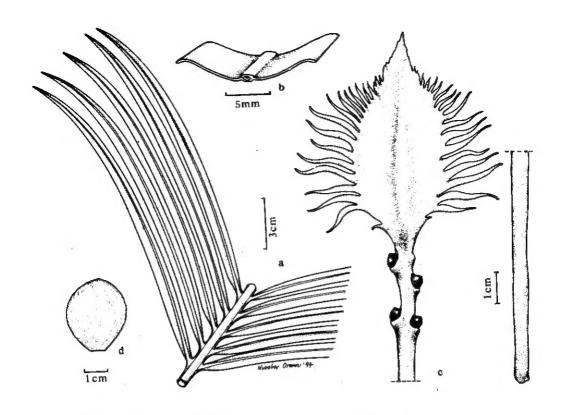


Fig. 6 Cycas taiwaniana. a. part of frond; b. section of pinna; c. megasporophyll; d. seed (all from C. J. Chen 88377). Scale bar; a=3 cm; b=5 mm; c=1 cm; d=1 cm

are from cultivated plants. Little is known about the habitat of the natural occurrences, and C. taiwaniana is now believed to be extinct in the wild. Reports of C. taiwaniana from Taiwan are the result of the misapplication of this name to the Taiwan cycad (Shen et al. 1994).

Notes: Distinguishing characteristics are discussed above under C. hainanensis.

Selected specimens; Guangdong; Gaoyao County, Shi 12204 (IBSC); Pingyuan County, Deng 68300 (IBSC), Deng 4410 (IBSC); Ruyuan County, Tan 321 (IBSC), Tan & Huang 321 (IBSC); Wengyuan County, Lau 2653 (IBSC), Lau 24847 (IBSC); Dinghu Shan, Zhaoqing County, Xie & Li 00156 (IBSC). Cult: Fujian, Xiamen, Lin 2916 (IBSC); Guangdong, C. J. Chen 88377 (PE).

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Plate 1



Holotype of Cycas taiwaniana Carruthers (BM 14112).